American Fern Journal 101(2):117–124 (2011)

New and Improved Leaf Terminology for Gleicheniaceae

SHANE W. SHAW and TOM A. RANKER
University of Hawai'i at Manoa, 3190 Maile Way, Room 101, Honolulu, Hawai'i 96822

ABSTRACT.—The majority of ferns have determinate leaf ontogeny, which makes them suitable for a hierarchal system of leaf terminology to describe dissection and gross morphology. Gleicheniaceae are distinct among fern families because nearly all species have indeterminate and pseudodichotomously forking leaves. Given these two characteristics, the hierarchal system of leaf terminology is inappropriate and cumbersome to use. Therefore, Holttum (1957), Tryon and Tryon (1982), Andersen and Øllgaard (1996), and Lellinger (2002), among others, developed specialized leaf terminology to describe the morphology of Gleicheniaceae leaves. Although each system is sufficient, comparisons among the different systems are cumbersome and confusing. To reduce confusion and simplify, we propose a new leaf terminology system that: 1) is universal to all taxa in Gleicheniaceae, 2) is more useful to apply to partial-leaf herbarium specimens, and 3) clarifies the ambiguity of having multiple leaf terminology systems.

KEY WORDS.—*Gleicheniaceae*, *Dicranopteris*, *Diplopterygium*, *Gleichenella*, *Gleichenia*, *Sticherus*, *Stromatopteris*, leaf terminology, frond terminology, fern

Fern leaf terminology is mostly a hierarchal system that describes a leaf from its base to its tip (Gifford and Foster, 1989; Andersen and Øllgaard, 1996) except for the terms penultimate and antepenultimate which are used to describe the second and third segment basiscopically from the ultimate segment, respectfully. This system works perfectly on the majority of ferns that have determinate leaves (i.e., those that stop growing once they reach maturity). But out of the 37 fern families recognized by Smith *et al.* (2006, 2008), Lygodiaceae and five of the six genera of Gleicheniaceae (i.e., *Dicranopteris, Diplopterygium, Gleichenella, Gleichenia,* and *Sticherus*) have indeterminate leaf growth, due to the repeated breaking of dormancy of the rachis bud, and pseudodichotomously forking pinna (Tryon and Tryon, 1982). Furthermore, under certain conditions, such as damage to or the removal of the rachis bud, some Gleicheniaceae species pinna buds may be reactivated, breaking dormancy and continue to grow (Holttum, 1957). This renders the hierarchal terminology inappropriate because the leaves continue to grow and become more complex over time.

Gleicheniaceae can have considerably large leaves; for example, some species are reported to have leaves that are up to 10 meters long (Gifford and Foster, 1989), with some species growing in dense thickets and scrambling over trees and shrubs (Holttum, 1954), thus making it nearly impossible to collect a whole leaf. Furthermore, botanists usually collect only enough plant material that will fit onto a herbarium sheet, so they will either collect a small portion of a leaf or a small juvenile individual. Both of these sampling techniques lead to incomplete herbarium specimens, which makes it difficult

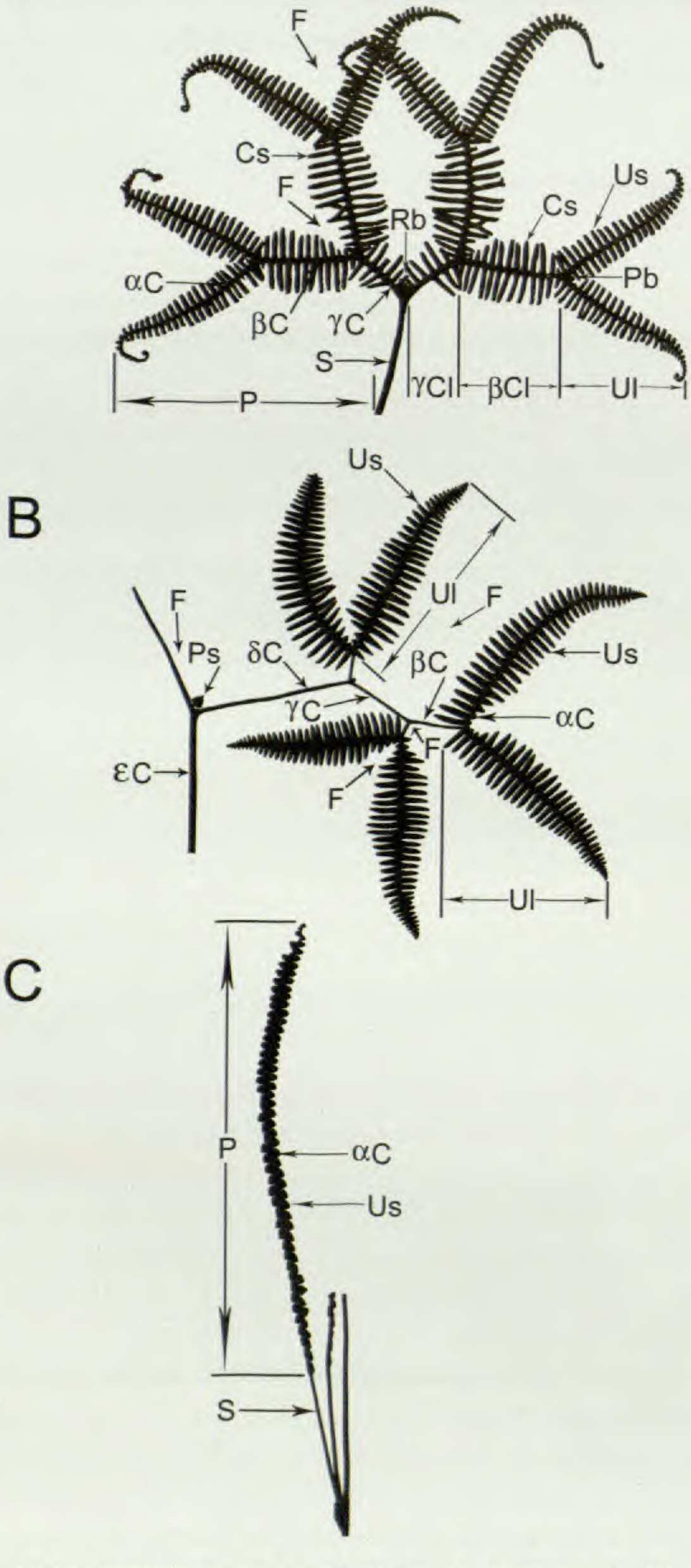

FIG. 1. Illustrations of Gleicheniaceae leaf terminology. A. *Sticherus* B. *Gleichenella* C. *Stromatopteris* D. *Dicranopteris* E. *Diplopterygium* F. *Gleichenia*. **Ac** = Accessory Costa **Al** = Accessory Leaflet, (**α,β,γ,δ,ε**) **C** = Costa, (**β,γ**) **Cl** = Costal Lamina, **Cs** = Costal Segment, **F** = Fork of pinnae, **P** = Pinna, **Pb** = Pinna Bud, **Ps** = Pseudostipule, **Ul** = Ultimate Leaflet, **Us** = Ultimate Segment, **Rb** = Rachis Bud, **S** = Stipe. Images modified from Smith (1981), Sampson (1985), and Palmer (2003).

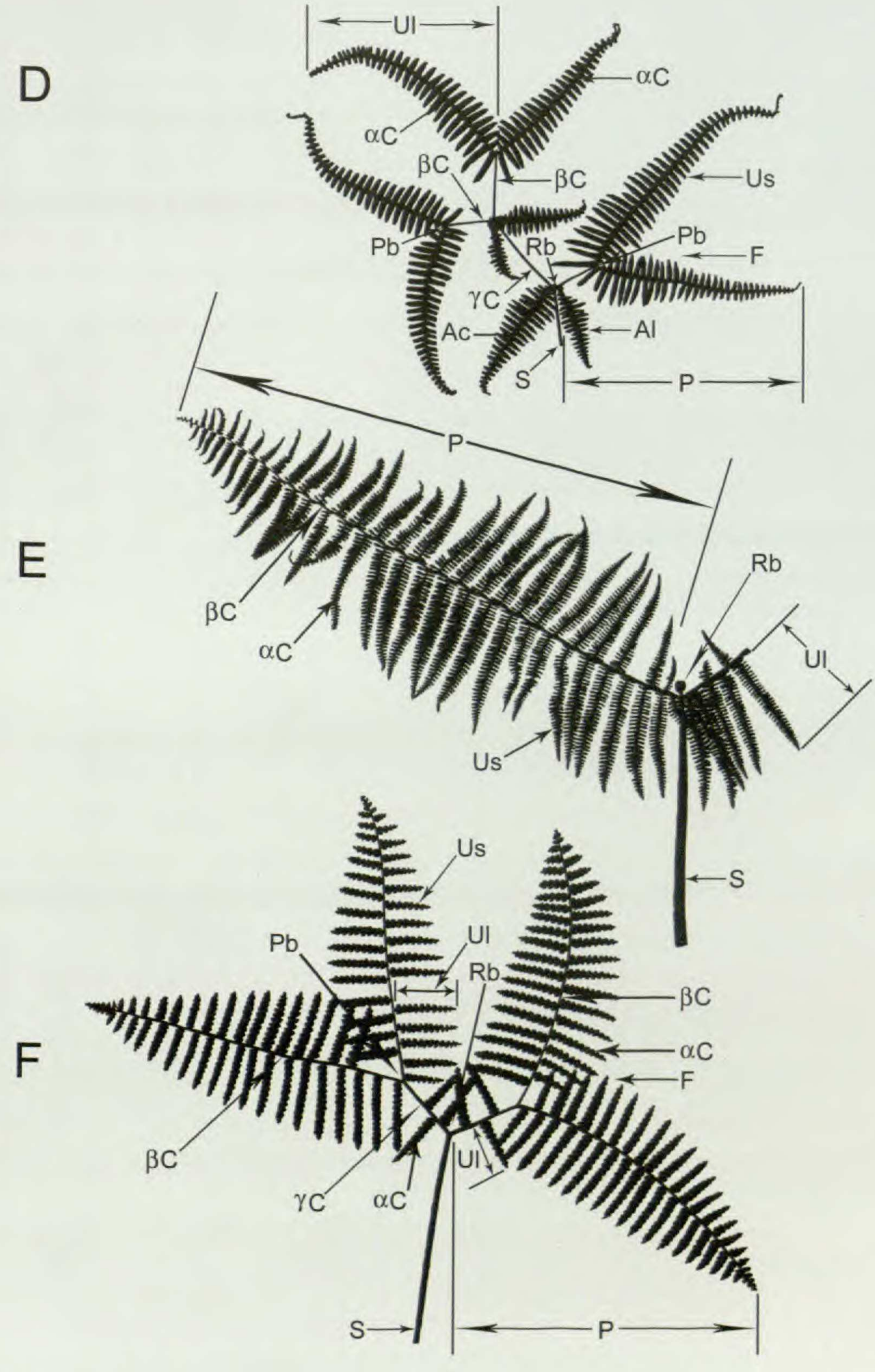

FIG. 1. Continued.

TABLE 1. Comparisons between Gleicheniaceae leaf terminology systems. Equivalent terms are read across the rows. ***** = Author did not have an equivalent term or did not define the term in their system.

Shaw and Ranker 2011	Lellinger 2002	Andersen and Øllgaard 1996	Tryon and Tryon 1982	Holttum 1957	Nakai 1950
Leaf	Frond	Leaf	Leaf	Frond	Frond
Lamina	Lamina	Lamina	Lamina	Lamina	Pinnule
Stipe	Stipe	*****	Petiole	*****	Stipe, Axis of the frond
Rachis	Rachis	Rachis	Rachis	Rachis, Main rachis, Main axis of the frond	Axis of the frond
Rachis bud	Dormant bud, Latent bud	Rachis bud, Dormant rachis	Rachis bud, Periodically dormant bud, Dormant bud, Leaf bud	Dormant Rachis-apex, Periodic dormancy of the apex of the main rachis, Dormant apex of main rachis, Dormant axis, Leading axis	*****
Pinna	Pinna, Branches	Pinna, Branch pair, Branch	Pinna, Lamina, Primary branch of lamina	Leaves, Primary branches, Frond branches, Primary rachis-branches, Branches of the first order, Lateral branches	Branch, Pinna, Leaves
Pinna bud	Dormant Bud, Latent Bud	Dormant bud, Bud	Periodically dormant bud, Permanently arrested bud, Laminar bud	Permanent dormancy of apices of secondary and lateral branchings, Dormant apex, Permanent dormant apex	Scaly bud
(α,β,γ,δ,ε) Costa	Costa, Costule, Costulet, Penultimate (branch), Antipenultimate (branch)	Costa, Branches that do not bear segments, Branches, Pinnules, Proximal branch orders, Lower levels of branching	Branches, Pinnate branch, Pinna-rachis, naked axis, axes of lower order, Lamina branches, Petiole	Primary rachis-branch, Costa, Primary branches, Secondary, tertiary, fourth order branches, Branches of the first, second, third, fourth, etc., order, Penultimate branches, Lateral branch, Axes of lower order, Branches, axes immediately beyond the forks	Axis of the frond, Rachis, Terminal branch, Costa, Rachides, Branchlets, Right-handed, left-handed, middle branchlet, Terminal branchlet, ultimate branchlets, Segments, Lateral branches

TABLE 1. Continued.

Shaw and Ranker 2011	Lellinger 2002	Andersen and Øllgaard 1996	Tryon and Tryon 1982	Holttum 1957	Nakai 1950
Costal lamina	Lamina, Segment	Segments	Pinnatisect penultimate segments	Leaflet, Axes of lower order that are leafy, Leafy lamina	Pectinate lobes (on axis of frond), basal pinnules
Costal segment	Segment	Segments	Ultimate segment, Penultimate segment	Lobe, Lamina-lobe, Lateral leaflets	Lobe, Pinnules, Leaf-segments
Ultimate leaflet	Ultimate branch	Ultimate branch	Ultimate branch	Leaflet, Lateral branch, Ultimate branch	Terminal pair of pinnae, Terminal branches, pinnae, Ultimate pinnules, Ultimate branchlets
Ultimate segment	Segment	Segment	Ultimate segment, Primary segments	Lobe, Lamina-lobe, Lateral leaflet	Lobe, Ultimate lobe, Pinnules, Leaf-segments
Pseudostipules	Pseudostipules	Pseudostipules	Stipular segments	Lobed leaflet	Aphlebia
Accessory leaflet	Sessile accessory branch	Accessory branch	Accessory branch	Accessory branch, Leaflet	Basal Pinnule
Accessory costa	*****	*****	*****	*****	*****
Midvein	Midvein	Midvein	*****	Midrib, Costule	Midrib, costa
Vein	Vein	Veinlet, Veinlet groups	Vein	Vein	Vein, Veinlet
Fork	Branched, Bifurcate	Pseudodicotomies, Branchings, Dichotomies	Pseudodicotomiesly Branched, fork, Pseudodichotomous	Branching pattern, Branched, Leaf branching, Pseudo-dichotomy, forking, forks	Forked, Dichotomously compound, Frond ladderly compound, Forking
Lobe	Lobe, Lobate	Lobe	*****	Slightly lobed	Lobe

or impossible to compare different taxonomic systems and in some cases apply the hierarchal system of leaf terminology.

Due to the atypical leaf development of Gleicheniaceae, many authors have developed specialized leaf terminology to describe the morphology of Gleicheniaceae leaves. The most cited systems are those of Nakai (1950), Holttum (1957), Tryon and Tryon (1982), Lellinger (1989, 2002), and Andersen and Øllgaard (1996). Although each system describes the morphology of the leaf adequately, each system could use improvement since some of the terms are confusing, especially to non-experts. For example, Nakai (1950), Holttum (1957), and Tryon and Tryon (1982) used terms such as "ultimate branch", "fourth order branches", and "right-handed branchlet" when they described how the pinnae pseudodichotomously split or the number of bifurcations that are in a single pinna.

Another problem occurs when one tries to compare two or more leaf terminology systems. Since each author coined their own terms, they sometimes used a different term for an identical part to which a different term had already been applied by another worker (e.g., Holttum's (1957) lobed leaflet is the same leaf appendage as Tryon and Tryon's (1982) stipular segment). In addition, different authors have used the same term to describe different parts (e.g., a lobe sensu Holttum's (1954) does not equal a lobe sensu Andersen and Øllgaard (1996)). Consequently, comparisons among the different Gleicheniaceae treatments can be unwieldy and perplexing.

Finally, some terminological systems do not apply to all six genera within Gleicheniaceae. For example, when Bierhorst (1971) constructed his leaf terminology system, he believed that *Stromatopteris* should not be assigned to Gleicheniaceae, but should be in its own family (Stromatopteridaceae). Therefore, he did not include *Stromatopteris* in his Gleicheniaceae leaf terminology system and used different terms to describe *Stromatopteris* leaf morphology. Since that time, molecular data have shown that *Stromatopteris* is within the Gleicheniaceae clade (Smith *et al.* 2006, 2008; Schuettpelz and Pryer, 2008) and, thus, it should be included under a Gleicheniaceae leaf terminology system. *Stromatopteris moniliformis* Mett. and *Gleichenia simplex* (Desv.) Hook. both have simple pinnatifid leaves, as well as a few other species that have less complex leaf architecture than normally found within the Gleicheniaceae, but to keep the terminology uniform throughout family, we applied the same terms used throughout, even though the conventional terminology works well on these species.

To address these problems, we propose a new leaf terminology system that is universal to all taxa in Gleicheniaceae and will facilitate working with partial-leaf herbarium specimens.

Unlike all other Gleicheniaceae leaf terminology systems, the one we propose starts from the distal tips of the pinna and continues proximally to the leaf base. Although this direction of description is unconventional, it works satisfactorily on Gleicheniaceae's atypical leaf growth and on incomplete herbarium specimens.

The following is a glossary of the terms we have adopted for this terminology system. Figure 1 illustrates how these terms apply to each genus in

Gleicheniaceae. The terms are a mixture of those assimilated and modified from those of earlier authors (especially Andersen and Øllgaard's (1996) and Lellinger's (2002)) and novel terms that we have coined. Table 1 is a comparison of the major Gleicheniaceae leaf terminology systems over the past 60 years compared to our new system. Each author's leaf term has been aligned in accordance with our new system. This will facilitate quick comparisons among all the different treatments and aid in understanding which part each term represents. The terms we used in our leaf system are based on the following conditions: the terms are functional for all taxa of Gleicheniaceae; they are applicable to incomplete herbarium specimens; and the terms are explicit and precise to simplify Gleicheniaceae leaf terminology.

Glossary

Accessory Costa: the major axis of the accessory leaflet.

Accessory Leaflet: supplementary lamina division that is borne basiscopically near a fork in the **(α,β,γ,δ,ε)** costae, such as the sessile leaflets subtending larger portions of the pinnae in some *Dicranopteris* species.

(α,β,γ,δ,ε) Costa: the major axis of the pinna. Subdivided by forking into equal or unequal sections. Each subsection is designated by a Greek letter starting from the apex (ultimate leaflet) and proceeding proximally towards the rachis/stipe.

Costal Lamina: the expanded portion of a leaf located on β, γ, δ, and/or ε costae, usually consisting of costal segments or lobes. Not always present because β, γ, δ, and/or ε costae may be naked.

Costal Segment: a portion of a costal lamina that is fully adnate to β, γ, δ, and/or ε costae and with deep sinuses on each side and that extends more than fifty percent of the segment length. *Cf.* Lobe.

Fork: a division in the pinna of two equal or unequal sections.

Lobe: a portion of the ultimate segment, costal lamina, accessory leaflet, or pseudostipule that is fully adnate to β, γ, δ, and/or ε costae, and/or accessory costae and with a shallow sinus on either side that extends less than fifty percent of the lobe length. *Cf.* Ultimate segment and Costal segment.

Midvein: the central axis of an ultimate segment or costal segment.

Pinna: the primary division of the leaf, that typically narrows at its base.

Pinna Bud: a bud borne at the apex of a costal axis that is flanked by two younger costal axes. Normally this bud stays dormant.

Pseudostipule: a small, foliaceous, stipule-like structure borne within a fork that subtends and protects a pinna bud.

Rachis: the central axis of a compound leaf.

Rachis Bud: a bud borne at the apex of the rachis that is flanked by two pinnae. This bud may break dormancy allowing the leaf to continue to develop.

Stipe: the central axis of a leaf that connects the base of the lamina to the rhizome.

Ultimate Segment: a portion of an ultimate leaflet, that is fully adnate to an α costa with deep sinuses on each side and that extends more than fifty percent of the segment length. *Cf.* Lobe.

Ultimate Leaflet: the smallest or last order of division of the pinna. Usually borne on a β costa, but in some species can be found on γ, δ, and/or ε costae.
Vein: a strand of vascular tissue, especially one in the laminar tissue of the ultimate segment or costal segment. Usually forked one or more times.

This top-down system simplifies Gleicheniaceae leaf terminology by being applicable to all taxa in Gleicheniaceae and to partial-leaf herbarium specimens. Finally, it reduces the perplexity of having more than one Gleicheniaceae leaf terminology system.

ACKNOWLEDGMENTS

We thank the Ranker Lab members (and extended family) for their comments on the leaf terminology system, MO, NY, and UC for specimen loans, and the reviewers for the comments and suggestions. SWS thanks the University of Hawai'i Department of Botany, Westmore Association, and Westmore Ladies Aid Society for financial support.

LITERATURE CITED

ANDERSEN, E. Ø. and B. ØLLGAARD. 1996. A note on some morphological terms of the leaf in the Gleicheniaceae. Amer. Fern J. 86:52–57.

BIERHORST, D. W. 1971. *Morphology of Vascular Plants.* The Macmillan Co., New York.

GIFFORD, E. M. and A. S. FOSTER. 1989. *Morphology and Evolution of Vascular Plants.* Third Edition. W. H. Freeman and Company, New York.

HOLTTUM, R. E. 1954. *A revised Flora of Malaya: an illustrated systematic account of the Malayan flora, including commonly cultivated plants.* Second Edition. Government Print Office, Singapore.

HOLTTUM, R. E. 1957. Morphology, growth-habit, and classification in the family Gleicheniaceae. Phytomorphology 7:168–184.

LELLINGER, D. B. 1989. *The Ferns and Fern–allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae).* American Fern Society, Washington.

LELLINGER, D. B. 2002. *A Modern Multilingual Glossary for Taxonomic Pteridology.* American Fern Society, Washington.

NAKAI, T. 1950. A new classification of Gleicheniales. Bulletin of the National Science Museum Tokyo 29:1–71.

PALMER, D. D. 2003. *Hawai'i's Ferns and Fern Allies.* University of Hawai'i Press, Honolulu.

SAMPSON, B. F. 1985. *Early New Zealand Botanical Art.* Reed Methuern Publishers, Auckland.S-Scanned by www.nzetc.org.

SCHUETTPELZ, E. and K. M. PRYER. 2008. Fern Classification. Pp. 395–416, *in*: T. A. Ranker and C. H. Haufler, eds. *Biology and Evolution of Ferns and Lycophytes.* Cambridge University Press, Cambridge.

SMITH, A. R. 1981. *Flora of Chiapas. Part 2 Pteridophytes.* California Academy of Science, San Francisco.

SMITH, A. R., K. M. PRYER, E. SCHUETTPELZ, P. KORALL, H. SCHNEIDER and P. G. WOLF. 2006. A classification for extant ferns. Taxon 55:705–731.

SMITH, A. R., K. M. PRYER, E. SCHUETTPELZ, P. KORALL, H. SCHNEIDER, P. G. WOLF and P. 2008. Fern Classification. Pp. 417–467, *in*: T. A. Ranker and C. H. Haufler, eds. *Biology and Evolution of Ferns and Lycophytes.* Cambridge University Press, Cambridge.

TRYON, R. M. and A. F. TRYON. 1982. *Ferns and Allied Plants with Special Reference to Tropical America.* Springer–Verlag, New York.